Analysis of ongoing neuronal activity evoked by continuous speech with computational corpus linguistics methods

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Abstract

In the field of neurobiology of language, neuroimaging studies are generally based on stimulation paradigms consisting of at least two different conditions. Depending on the desired evaluation, these conditions, in turn, have to contain dozens of items to achieve a good signal to noise ratio. Designing those paradigms can be very time-consuming. Subsequently, a group of participants is stimulated with the new paradigm, while brain activity is assessed, e.g. with EEG/MEG. The measured data are then pre-processed and finally contrasted according to the different stimulus conditions. In this way, only a limited number of analyses and hypothesis tests can be performed, while for alternative or further analyses, completely new paradigms usually need to be designed. This traditional approach is necessarily data-limited, and the cost-benefit ratio is therefore rather poor. In contrast, in computational linguistics analyses are based on text corpora, which allow a vast variety of hypotheses to be tested by repeatedly re-evaluating the data set. Furthermore, text corpora also allow exploratory data analysis in order to generate new hypotheses. By combining the two approaches, we here present a unified approach of continuous natural speech and MEG to generate a corpus-like database of speech-evoked neuronal activity.

Introduction

Contemporary linguistic research is characterized by a great variety of different methodological approaches. The fields of psycholinguistics and neurobiology of language in particular are characterized by a vast number of different methods that are applied in order to investigate the neuronal and cognitive correlates and processing principles of language acquisition, representation, comprehension and production [1]. In neurolinguistics, electrophysiological measurements, i.e. magnetoencephalography (MEG) [2] and electroencephalography (EEG) [3, 4], are widely used to investigate the neural correlates of language processing in the human brain [5–10].

However, most of the experimental studies on language processing conducted so far have focused on one aspect of language information at a time. For instance, neurocognitive studies have explored the brain responses of words against pseudo words [11, 12], between different conceptual semantic categories [13], complex against simple grammatical sentences [14] or during pragmatic processing of different communicative actions [10]. Although, all these studies shed light on the correlates of language processing in the human brain, it is still not fully understood whether similar brain responses during single words or sentence understanding also emerge during perception of natural speech, similar to everyday experience. However, recently a growing number of approaches address this issue [15–20].

Furthermore, traditional experimental designs typically consist of at least two different conditions studied under carefully controlled circumstances [7–9]. The measured data are then pre-processed, i.e. referenced, filtered, epoched and averaged, and finally contrasted according to the different stimulation conditions [1]. To have a good signal to noise ratio (SNR) of the acquired brain responses each of these conditions must contain dozens of different items or stimulus repetitions.

For instance, the evaluation of event related potentials (ERPs) from the EEG data, or, in the case of MEG, event related fields (ERFs), requires a relatively large number of stimuli (40-120 trials) per condition to achieve high SNR and ensure sufficient statistical power. This is due to the fact that the signal of a specific condition remains constant across multiple repetitions while the noise signal which is assumed to be randomly distributed, is reduced when large number of time-locked stimuli are pooled together [21–25]. Apart from creating a large number of stimuli to increase SNR, it is also well known that neural activity is reduced by stimulus repetition, the so-

called repetition suppression [26]. Thus, it is necessary to design a certain number of different stimuli from each condition to avoid repetition, which is often very challenging or even impossible. One strategy is to focus on single-item ERPs/ERFs, but here it is necessary to compensate by testing more participants to obtain stable signals [27].

Here, we present an alternative approach to overcome the aforementioned limitations of electrophysiological language assessment and open up the possibility of investigating different levels of linguistic information during natural speech comprehension within a single experiment. In particular, in the present study, we investigated brain responses elicited during listening to a German novel (audiobook) by means of MEG measurements (for similar approaches see [28, 29]). Using computational corpus linguistics (CCL) [30, 31] applied to the analyses of large text corpora, which usually consist of hundreds of thousands or even billions of tokens [32–37], offers the opportunity to test a vast number of hypotheses by repeatedly re-analyzing the data [38] and to deploy modern machine learning techniques on such datasets [39]. Furthermore, text corpora also allow for exploratory data analyses in order to generate new hypotheses [40]. Thus, in our approach in a single measurement session, we can generate a large database of neuronal activity corresponding to the comprehension of several thousands of words of continuous speech similarly to everyday language. However, for later studies the data set has to be split into multiple parts (e.g. development/training/test or training/validation/test) in analogy to standard machine learning data sets as MNIST (50,000 training images, 10,000 test images [41]), as hypothesis generation and checking for statistical significance have to be done in two disjoint steps, in order to prevent *harking* (hypothesizing after the results are known) [42]. In such cases, inferential statistical analysis is not valid and applicable [43]. Thus, this approach is only possible with a large dataset.

Here, we provide the proof-of-principle of this approach by calculating ERFs and normalized power spectra of word onsets and offsets overall as well as for the group of content words (nouns, verbs, adjectives) and for the group of function words (determiners, prepositions, conjunctions), as they differ semantically to a substantial extent. Hence, greater activation for content compared to function words can be expected, as reported in previous studies (e.g., [44, 45]). Furthermore, we check for consistency of the data, by comparing intra-individual differences of neural activity in different brain regions and we performed non-parametric cluster permutation tests to determine significant differences between conditions.

Methods

Human participants

Participants were 15 (8 females, 7 males) healthy right-handed (augmented laterality index: $\mu = 85.7$, $\sigma = 10.4$) and monolingual native speakers of German aged 20-42 years. They had normal hearing and did not report any history of neurological illness or drug abuse. They were paid for their participation after signing an informed consent form. Ethical permission for the study was granted by the ethics board of the University Hospital Erlangen (registration no. 161-18 B). For the questionnaire based assessment and analysis of handedness we used the Edinburgh Inventory [46].

Speech stimuli and natural language text data

As natural language text data, we used the German novel *Gut gegen Nordwind* by Daniel Glattauer (© *Deuticke im Paul Zsolnay Verlag*, Wien 2006) which was published by *Deuticke Verlag*. As speech stimuli, we used the corresponding audiobook which was published by *Hörbuch Hamburg*. Both, the novel and the audiobook are available in stores, and the respective publishers gave us permission to use them for the present and future scientific studies.

Book and audiobook consist of a total number of 40460 tokens (number of words) and 6117 types (number of different words). The distribution of uni-gram word classes and bi-gram word class combinations occurring in the text were analysed by applying *part-of-speech (POS) tagging* [47, 48] as implemented in the python library *SpaCy* [49]. The results are summarized in Figure 1.

The total duration of the audiobook is approximately 4.5 hours. For our study, we only used the first 40 minutes of the audiobook (that corresponds to approximately 6000 words of spoken language), divided into 10 parts with approximately 4 minutes duration ($\mu = 245\,s$, $\sigma = 39\,s$). In order to avoid cutting the text in the middle of a sentence or even in the middle of a word, we chose the borders of the 10 parts in such a way that it results a meaningful interruption of the text.

Stimulation protocol

The continuous speech from the audiobook was presented in 10 subsequent parts (cf. above) at a sensory level of approximately 30-60 dB SL. The actual loudness varied from participant to participant. It was chosen individually to ensure good intelligibility during the entire measurement, but also to prevent it from being unpleasant. Simultaneously with auditory stimulation, a fixation cross at the centre of the screen was presented all the time to minimize artifacts from eye movements. After each audiobook part, three multiple-choice questions on the content of the previously presented part were presented in order to test the participants' attention. Furthermore, stimulation was interrupted for a short break of approximately 5 minutes after audiobook parts number 4 and 7. The total duration of the protocol is approximately one hour. The complete stimulation protocol is shown in Figure 2.

Generation of trigger pulses

In order to automatically create trigger pulses for both, the synchronization of the speech stream with the MEG recordings, and to mark the boundaries of words, phonemes, and silence for further segmentation of the continuous data streams, *forced alignment* [50–52] was applied offline. For this study we used the free web service *WebMAUS* [53, 54]. It takes a wave file containing the speech signal, and a corresponding text file as input and gives three files as output: the time tags of word boundaries, a phonetic transcription of the text file, and the time tags of phoneme boundaries. Even though, forced alignment is a fast and reliable method for automatic phonetic transcription of non-prompted speech, we carried out random manual inspections in order to ensure that the method actually worked correctly. For simplicity, we only used the time tags of word boundaries in this study. However, a more fine grained analysis on the level of phonemes could easily be performed retrospectively, since the time tags of beginning and ending of a given word correspond to the beginning of the word's first phoneme and the ending of the word's last phoneme, respectively. Thus, the two lists containing the time tags of the word and phoneme boundaries can easily be aligned with each other.

Setup for speech presentation and synchronisation with the MEG recordings

The speech signal was presented using a custom made setup (Figure 3). It consists of a stimulation computer connected to an external USB sound device (Asus Xonar MKII, 7.1 channels) providing five analog outputs. The first and second analog outputs are connected to an audio amplifier (AIWA, XA-003), where the first output is connected in parallel to an analog input channel of the MEG data logger in order to enable an exact alignment of the presented stimuli and the recorded MEG signals (cf. Figure 3 a). In addition, the third analog output of the sound device is used to feed the trigger pulses derived from forced alignment into the MEG recording system via another analog input channel. In doing so, our setup prevents temporal jittering of the presented signal caused by multi-threading of the stimulation PC's operating system, for instance. For an overview of the wiring scheme of all devices see Figure 3a.

The speech sound was transmitted into the magnetically shielded MEG chamber to the participants' ears via a custom-made construction consisting of two loudspeakers (Pioneer, TS-G1020F) which are coupled to silicone funnels each connected to a flexible tube of $\approx 2\,m$ length and with an inner diameter of $\approx 2\,cm$ (Figure 3b). These tubes are led through a small hole in the magnetically shielded chamber to prevent artifacts produced by interfering magnetic fields generated by the loudspeakers (Figure 3c). We carried out calibration tests to ensure that the acoustical distortions caused by the tube construction do not affect speech intelligibility. Furthermore, due to the length of the tubes and the speed of sound, there is a constant time delay from the generation of sound to the arrival of the sound at the participant of $\approx 6\,ms$, which we took into account for the alignment described below.

The stimulation software is implemented using the programming language *Python 3.6*, together with Python's sound device library, the *PsychoPy* library [55, 56] for the stimulation protocol, and the *NumPy* library for basic mathematical and numerical operations.

Magnetoencephalography and data processing

MEG data (248 magnetometers, 4D Neuroimaging, San Diego, CA, USA) were recorded (1017.25 Hz sampling rate, filtering: 0.1-200 Hz analogue band pass, supine position, eyes open) during speech stimulation. Positions of five

landmarks (nasion, LPA, RPA, Cz, inion) were acquired using an integrated digitizer (Polhemus, Colchester, Vermont, Canada). MEG data were corrected for environmental noise using a calibrated linear weighting of 23 reference sensors (manufacturers algorithm, 4D Neuroimaging, San Diego, CA, USA).

Further processing was performed using the Python library *MNE* [57,58]. Data were digitally filtered offline (1-10 Hz bandpass for ERF analyses; 50 Hz notch on for power spectra analysis) and down sampled to a sampling rate of 1000 Hz. MEG sensor positions were co-registered to the ICBM-152 standard head model [59] and atlas 19-21 [60], as individual MRI data sets for the participants were not available. Furthermore, recordings were corrected for eye blinks and electrocardiography artifacts based on signal space projection of averaged artifact patterns, as implemented in *MNE* [57, 58].

Additionally, we performed an independent component analysis (ICA) and deleted the first two independent components of the data, to further improve data quality. However, it appears that this processing step does not affect the observed differences of neural responses to function and content words (Figures 7 and S10).

Trials with amplitudes higher than $2 \cdot 10^{-12}$ T would have been rejected, as they were supposed to arise from artifacts. However, none of the trials fit this condition, and hence no trail was rejected.

For this study, we restricted our analyses to sensor space, and did not perform source localization in analogy to other ERF studies [61–63].

Alignment and segmentation

Since we have both, the original audiobook wave file together with the time tags of word boundaries from forced alignment (Figure 4a), and the corresponding recordings of two analog auxiliary channels of the MEG (Figure 4b), all 248 MEG recording channels could easily be aligned offline with the speech stream (Figure 4c). Subsequently, the continuous multi-channel MEG recordings were segmented using the time tags as boundaries, and labeled with the corresponding types, in our case individual words (Figure 5). For the analysis of function and content words, we additionally applied POS tagging [47,48] using SpaCy [49] to assign word classes (nouns, verbs, adjectives, conjunctions, determiners, prepositions) to the individual words. Note that, in principle, the process of segmentation can also be performed at different levels of granularity. For instance, using the time tags of phoneme bound-

aries would result in a more fine-grained segmentation, whereas grouping several words together to n-grams with appropriate labels to larger linguistic units (i.e. collocations, phrases, clauses, sentences) would result in a more coarse-grained segmentation.

Event related fields

In order to provide the proof-of-principle of our approach, we analysed event related fields (ERF) evoked by word onsets (Figure 6). Since the continuous MEG signals of all 248 channels are already segmented according to word boundaries, we can compute ERFs of word onsets for each channel by simply averaging the pre-processed signals over the word tokens in our database. Here, we included only those words that follow a short pause, instead of using all words occurring in the data set. Thus, there is a short period of silence, ranging from *aprox* 50 ms to 1.5 seconds, before the actual word onsets which improves signal quality, yet with the drawback that only a fraction of all tokens can be used. However, there were still 291 remaining events, baseline corrected, within the first three parts of the audiobook, corresponding to $\approx 12\,min$ of continuous speech, that fit this condition.

In addition, we also analysed ERFs evoked by prototypical content words (nouns, verbs, adjectives) and compared them with ERFs evoked by function words (determiners, prepositions, conjunctions). Again, we included only those words that follow a short interval of silence, instead of using all words occurring in the data set. Within the first three parts of the audiobook, this resulted in 81 remaining events for the content word condition and 106 events for the function word condition.

Permutation test

We performed intra-individual permutation tests to determine the p-value for the ERF comparison between content and function word. Thus, the ERF was cut into four subsequent time frames, each with a duration of 250 ms, and the root-mean-square amplitude (RMS) was calculated (Figure 7e):

$RMS = \sqrt{\frac{1}{N}\sum_{i=0}^{N} v_i^2}$, with the signal values within a 250 ms interval v_i, the total number of values within a 250 ms interval $N = f_s \cdot 250\,\text{ms}$, and the sampling rate $f_s = 1000\,\text{Hz}$.

1000 different random permutations of content word and function word

labels were generated. For each of these samples the four RMS amplitudes for the different time frames were calculated based on the baseline corrected single trials, resulting in a distribution of amplitudes for each time frame (Figure 7f). The amplitude values corresponding to the true labeling are compared with amplitudes derived from random permutations in order to estimate the statistical significance, i.e. the p-values for content and function words p_{con} and p_{fun}, respectively, in Figure 7f.

Normalized power spectra

Using Fourier transformation, we also analyzed the averaged normalized power spectra (alpha, beta and gamma frequency range) for words in contrast to pauses, and for function and content words. The frequency band were defined as follows : $\alpha : 8 - 12\,\mathrm{Hz}$, $\beta : 12 - 30\,\mathrm{Hz}$, $\gamma : 30 - 45\,\mathrm{Hz}$. The epoch length for this analysis was 1 s for both, short periods of silence and word onsets. Furthermore, we projected the resulting values to the corresponding spatial position of the sensors. This was done by the usage of the plot_psd_topomap function of the *MNE* library with Python interface [57,58].

Results

The general idea of our approach was to perform MEG measurements of participants listening to an audiobook. By synchronizing the continuous speech stream with the ongoing multi-channel neuronal activity, and subsequently automatically segmenting the data streams according to word boundaries derived from forced alignment, we generated a database of annotated speech evoked neuronal activity. This corpus-like database may then be analyzed offline by applying the full range of methods from statistics, natural language processing, and computational corpus linguistics. In order to demonstrate the feasibility of our approach, we restricted our analyses to sensor space and did not perform any kind of source localization (cf. Methods). More specifically, we calculate averaged ERFs for word onsets, and normalized power spectra for onsets of both, words and short pauses. In addition, we compare averaged ERFs for content and function words, and the corresponding normalized power spectra and discuss the results in the light of existing studies.

Event related fields of word onsets

For a first proof of concept and to determine clear neurophysiological brain responses from continuous speech, we analyzed event related fields (ERFs) for word onsets (irrespective of their word classes) from different topographical sides.

Figure 6a shows one example of the resulting ERFs averaged over the aforementioned 291 events corresponding to word onsets for one participant (subject 2 of 15) and parts number 1 to 3 of the audiobook and Figure 6b shows a projection of the spatial distribution of the ERF amplitudes at 350 ms after word onset. The largest amplitudes occur in channels located at temporal and frontal areas of the left hemisphere known to be associated with language processing [64]. The ERFs of those channels with the largest ERF amplitudes are shown in Figure 6c. Furthermore, we see a clear N400 component for each condition, indicating language associated processing (cf. [17, 65–69]).

In order to exclude random effects, we compare these channels with the corresponding channels located at the right hemisphere – where we expect less activation due to the asymmetric laterilsation of speech in the brain – (Figure 6d), and with some occipital channels (Figure 6e). In both cases, the

resulting ERF amplitudes are clearly smaller than those of the left temporal and frontal channels (Figure 6c). In addition, we calculate control ERFs for the same channels shown in Figure 6c, but instead of word boundaries we used randomly chosen time tags for segmentation. Also in this control condition, the resulting ERF amplitudes are smaller than those for the word onset condition (Figure 6f). This result,in particular, demonstrates that even though there are no or only relatively short inter stimulus intervals, leading to overlapping effects of late and early responses of subsequent words, there is still enough signal left in the individual trials.

Finally, we evaluated the re-test reliability of our results using three-fold sub-sampling by separately averaging only over events belonging to the same part of the the audiobook (Supplemental Figures S1, S2, S3). Again, the largest ERF amplitudes were found in the same channels as before and all results show very similar patterns to those shown in Figure 6. In addition, we provide exemplary results of two further participants in the Supplements section (Supplemental Figures S4 and S5).

Event related fields of content and function words

As a further validity test of the present study, we analyzed and compared the brain responses of function words, defined as determiners, prepositions and conjunctions, and content words, defined as nouns, verbs and adjectives. We choose these lexical categories as they greatly differ in the semantic domain. As an example, the resulting ERFs averaged over the respective events (content words: n=81, function words: n=106) for one participant (subject 2 of 15) and parts number 1 to 3 of the audiobook are shown in Figure 7a,c. and a projection of the spatial distribution of the ERF amplitudes at 550 ms after word onset is provided in Figure 7b,d. We found that content words (Figure 7a,b) elicited greater activation than function words (Figure 7c,d), especially in temporal and frontal areas of the left hemisphere. Since content parts of speech have been shown to differ semantically from function parts of speech [70, 71], this finding is in line with previous studies [45]. In addition, we compared the two conditions for the channel yielding the largest ERF amplitude and performed a permutation test independently for four subsequent time frames each with a duration of 250 ms (Figure 7e,f). We found that the averaged ERFs for the two conditions (content and function words, intra-individual) are significantly ($p < 0.05$) different within the first (0 ms–250 ms) and third (500 ms–750 ms), but not within the second (250 ms–500 ms) and

fourth (750 ms–1000 ms) time frame (Figure 7f, two further subjects shown in Figures S6, S7).

Averaged normalized power spectra

We also analyzed the averaged normalized power spectra for the conditions of word onset and silence onset (Supplemental Figure S8), as well as content words and function words (Supplemental Figure S9). Here, we could not find any significant differences.

Discussion

In this study, we presented an approach where we combine electrophysiological assessment of neuronal activity with computational corpus linguistics, in order to create a corpus-like database of continuous speech-evoked neuronal activity. We demonstrated that using an audiobook as natural speech stimulus, and simultaneously performing MEG measurements led to a relatively large number of analysable events (word onsets: $n = 291$, zero-word onsets: $n = 187$, content words: $n = 81$, function words: $n = 106$), yet within a relatively short measurement time of $15\,min$. We further provided the proof-of-principle that, in contrast to common study designs, even though our stimulus trials were not presented in isolation, i.e. with appropriate inter-stimulus intervals of a few seconds, averaging over all respective events of a certain condition results in ERFs in left temporal and frontal channels with increased amplitudes compared to those of several control channels (e.g. at right hemisphere or at occipital lobe). The same is true with respect to comparison with control conditions (e.g. random trigger times). These results are well in line with previously published findings [64]. Furthermore, we analyzed ERFs for content words and function words. We found a clear N400 component (cf. Figure 7) especially in left hemispheric frontal regions for both function and content words and a positive component from 400-700 ms in good accordance with Brennan et al.'s findings [72, 73].

Additionally, we found that content words elicit greater activation than function words, especially in temporal and frontal areas of the left hemisphere. Due to their substantial semantic differences [70, 71], this finding is in line with previous studies [45].

We also analyzed the averaged normalized power spectra for the conditions of word onset and silence onset (Supplemental Figure S8), as well as content words and function words (Supplemental Figure S9). However, here we could not find significant differences. It was found that presentation of speech stimuli was associated with an increase in broadband gamma and a decrease in alpha over auditory cortex, while alpha power was increased in domain unspecific cortical areas [74–76]. One reason could be that, since we analysed only very short periods of silence, i.e. between two words, our two conditions of word onset and silence onset can be considered basically, at a larger time scale, to be the same condition, i.e. continuous speech stimulation. This may explain why we found no differences in frequency power here. Even though it has been proposed that in human language networks, differ-

ent types of linguistic information is transferred in different oscillatory bands – in particular attention is assumed to correlate with an increase in gamma and a decrease in alpha band power [77] –, the role of different spectral bands in mediating cognitive processes is still not fully understood. Therefore it remains unclear, whether these findings extend to content and function words. Whether our approach is too insensitive to see differences here remains to be seen, and further studies should look more closely at this issue.

As mentioned above, in contrast to traditional studies that are limited to testing only a small number of stimuli or word categories, the present approach opens the possibility to explore the neuronal correlates underlying different word meaning information across a large range of semantic categories [29], and syntactic structures [78]. This is because the ongoing natural speech used here contains both, a large number of words from different semantic domains [28] and a large number of sentences at all levels of linguistic complexity [79].

On the other hand, one may argue that stimulation with ongoing natural speech has, compared to traditional approaches, the drawback that there are virtually no inter stimulus intervals between the single words. This, of course, introduces a mixture of effects at different temporal scales, e.g. early responses to the actual word are confounded with late responses of the previous word. However, all these effects may be averaged out, as demonstrated by other studies [15–20] and also by our results.

In a follow-up study, it will have to be validated whether our approach also works for linguistic units of different complexity other than single words. For instance, smaller linguistic units like phonemes and morphemes, but also larger linguistic units like collocations, phrases, clauses, sentences, or even beyond, could be investigated. Furthermore, more abstract linguistic phenomena need to be analyzed, e.g. argument structure constructions [80–82] or valency [83–85]. Finally, our speech-evoked neural data may also be grouped, averaged, and subsequently contrasted according to male and female voice, looking at gender specific differences (see e.g., [86, 87]).

Also, analyses based on source space need to be tested, as well as more sophisticated analyses methods taking advantage of the multi-dimensionality of the data, such as, for instance, multi-dimensional cluster statistics [88] and state-of-the-art deep learning approaches for creating so-called embeddings of the raw data [89]. Due to the corpus-like features of our data, all additional analyses mentioned may be performed on the existing database, and without the need for designing new stimulation paradigms, or carrying out additional

measurements.

However, in order to avoid statistical errors due to *HARKing* [42, 43] - defined as generating scientific statements exclusively based on the analysis of huge data sets without previous hypotheses - and to guarantee consistency of the data, it is necessary to apply e.g. re-sampling techniques such as sub-sampling as shown above and described in detail in [90]. Furthermore, the approach presented here allows us to apply the well-established machine learning practice of dataset splitting, i.e. to split the dataset into multiple parts before the beginning of the evaluation, where the one part is used for generating new hypotheses, and another part for subsequently testing these hypotheses (or split again into training and testing data).

Finally, even though audiobooks are frequently used in similar studies [15–20], one may also discuss whether audiobooks actually can be considered natural speech. One could argue that the fact that highly trained professional speakers and actors are usually employed to read audiobooks, who may use specific intonational patterns to paint a more vivid image of the situation, may lead to unnaturalness and thus possibly to unusual arousal patterns in the hearer. However, this argument is flawed. People spend large portions of their days listening to language produced by such professional speakers for radio, television news and drama, online videos, and podcasts. While probably not predominant for most people, it corresponds to perfectly normal, everyday type of language experience. Of course, further studies using recordings of everyday dialogues between untrained subjects, e.g. describing what they have done during the day, should be designed to obtain a more comprehensive picture and more robust results, because, as Kriegeskorte and Douglas pointed out: *"As we engage all aspects of the human mind, our tasks will need to simulate natural environments"* [91]. A purely receptive task such as the one used in this study is one type of natural environment, but further natural environments, including spontaneous interaction, will have to be researched to verify the general validity of our results.

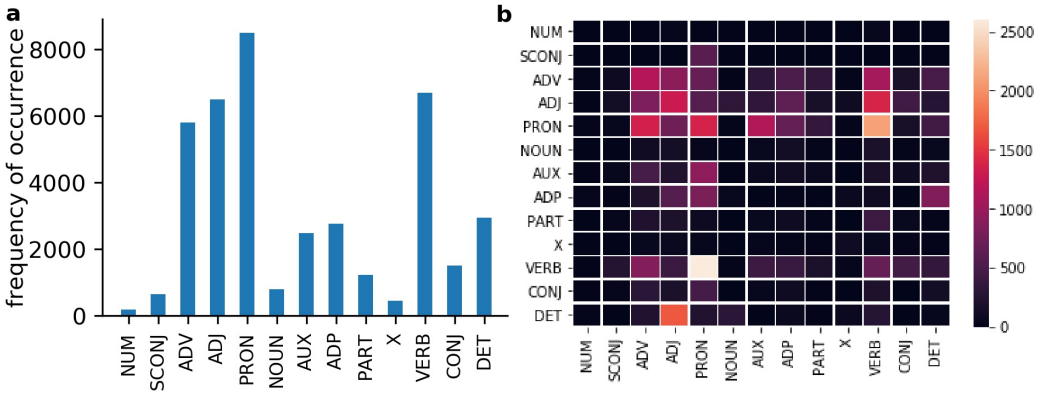

Figure 1: **Distribution of word classes and bi-gram word classes.** a: Distribution of word classes according to POS-tagging. Pronouns (PRON), verbs (VERB), adjectives (ADJ) and adverbs (ADV) are the most frequent word classes. The less frequent are: numbers (NUM), subordinating conjunctions (SCONJ), nouns (NOUN), auxiliary verbs (AUX), adpositions (ADP), particles (PART), conjunctions (CONJ), determiners (DET), and others (X). b: Distribution of word classes of 2-word sequences. The two most frequent sequence types are VERB-PRON and PRON-VERB. Rows: word class of first word. Columns: word class of second word.

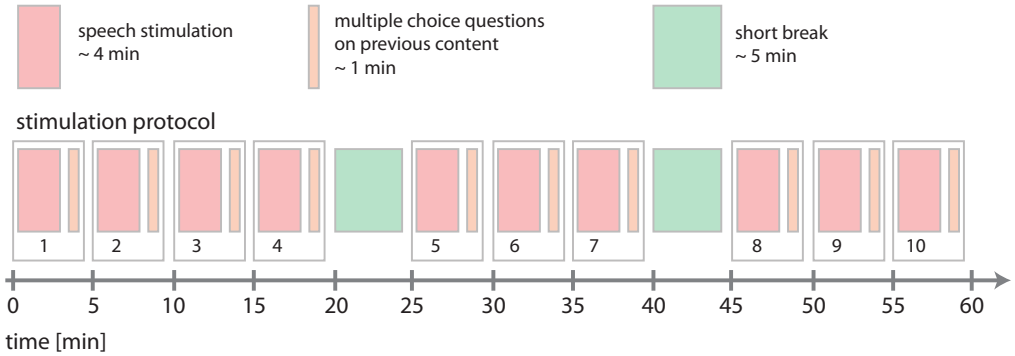

Figure 2: **Stimulation protocol.**
The total duration of the protocol was approximately one hour. The audiobook was presented in 10 subsequent parts with an average duration of 4 minutes (red). After each part, three multiple-choice questions on the content of the previous part of the audiobook were presented (orange). After audiobook parts number 4 and 7, stimulation was interrupted for a short break of approximately 5 minutes (green).

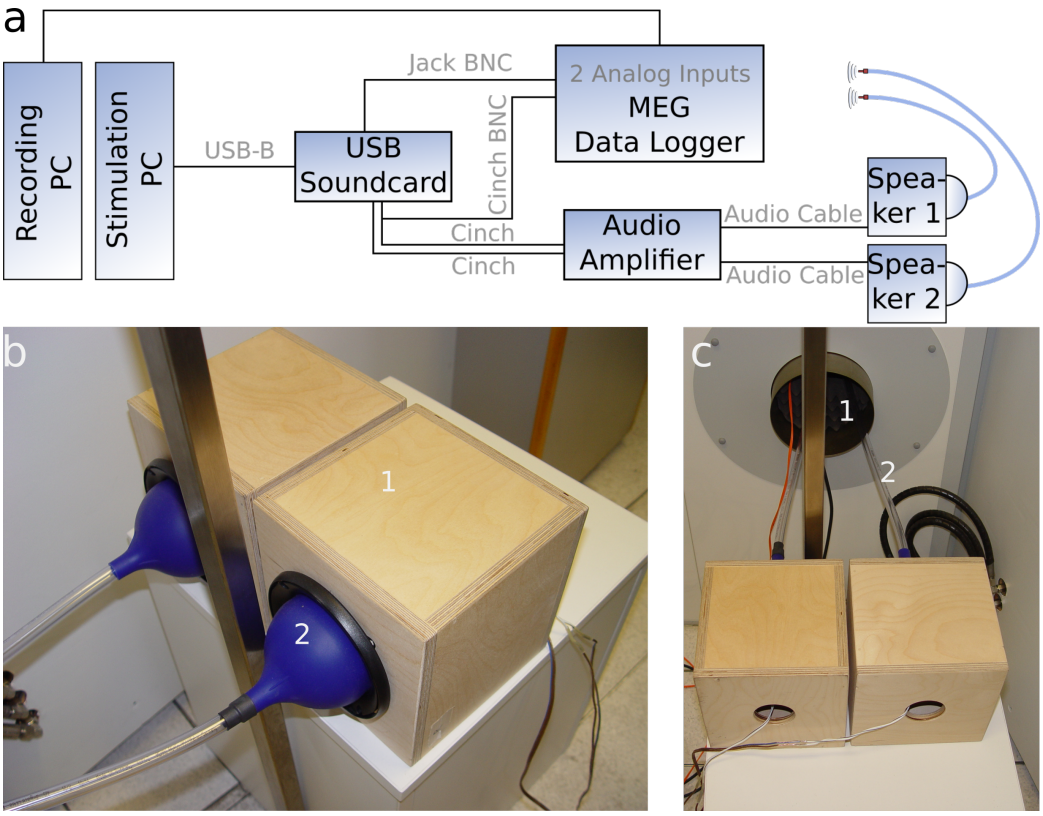

Figure 3: **Setup configuration.**
a: Wiring scheme of the different devices. b: The speech sound is transmitted into the magnetically shielded chamber via a custom-made construction consisting of two loudspeakers (1) which are coupled to silicone funnels (2) each connected to a flexible tube. c: Through a small whole in the magnetically shielded chamber (1), speech sound is transmitted via the two flexible tubes (2).

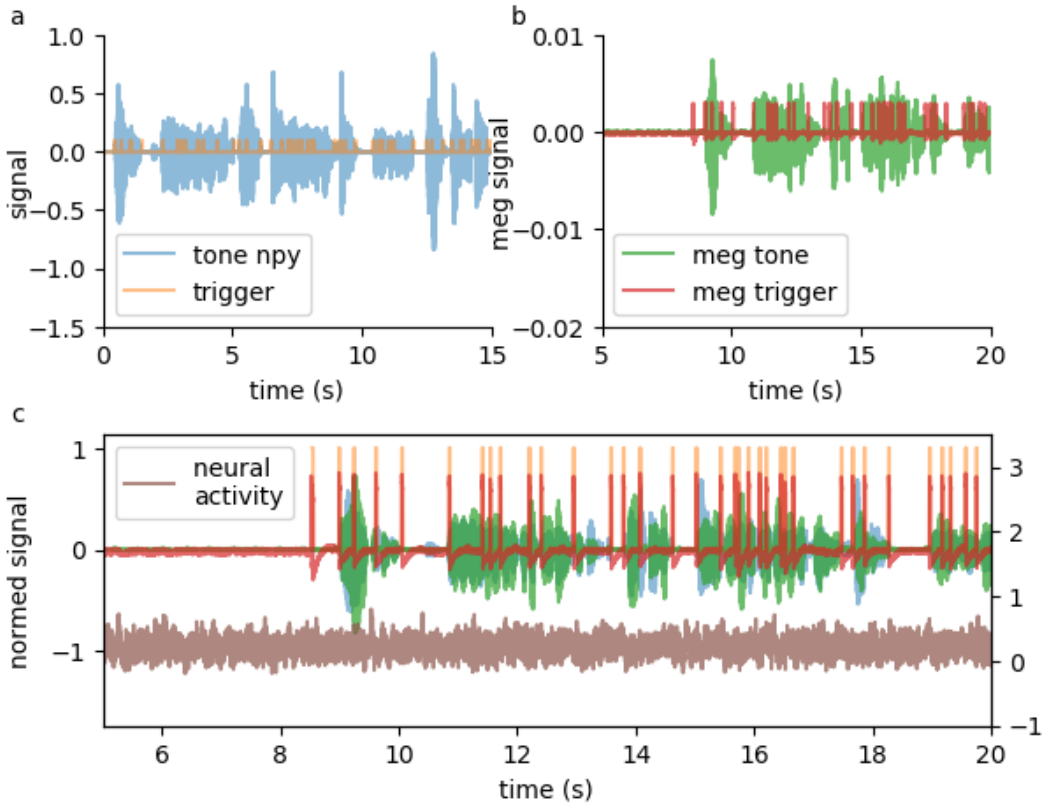

Figure 4: **Alignment of speech stream and MEG signal.**
a: Sample audiobook wave file (blue) together with time tags of word boundaries (orange) from forced alignment. b: Corresponding recordings of two analog auxiliary channels of the MEG. c: Alignment of data streams from a and b, together with one sample MEG channel.

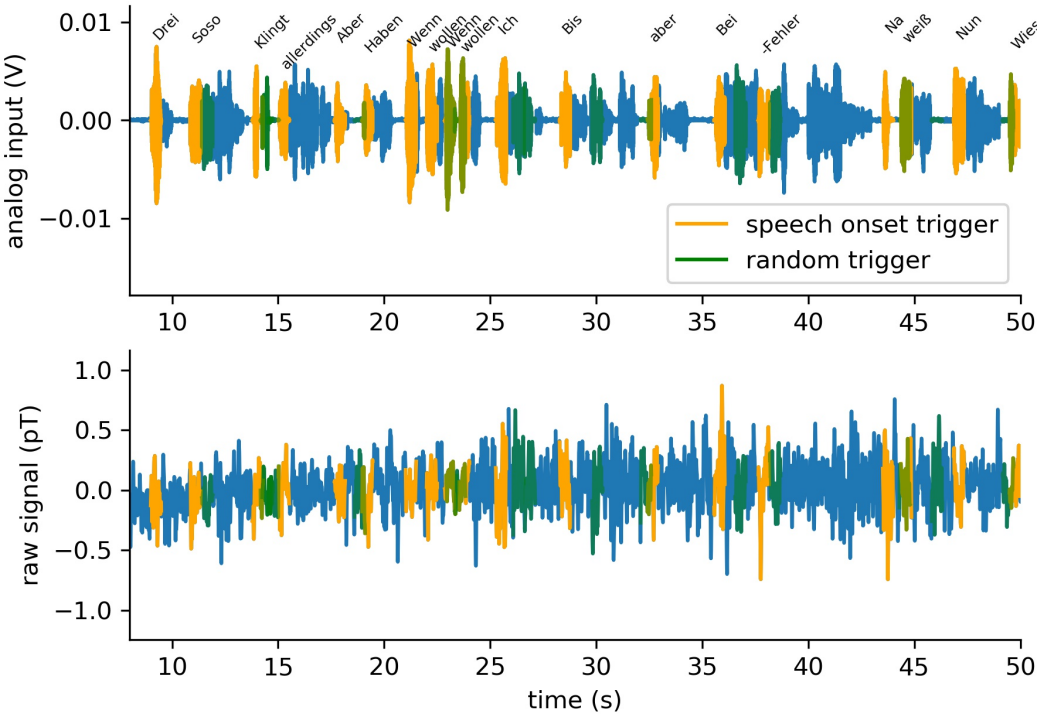

Figure 5: **Segmentation of speech stream and MEG signal.**
After alignment, the continuous wave file (top panel) and multi-channel MEG recordings (bottom panel) are segmented using the time tags from forced alignment as boundaries, and labeled with the corresponding types, i.e. words.

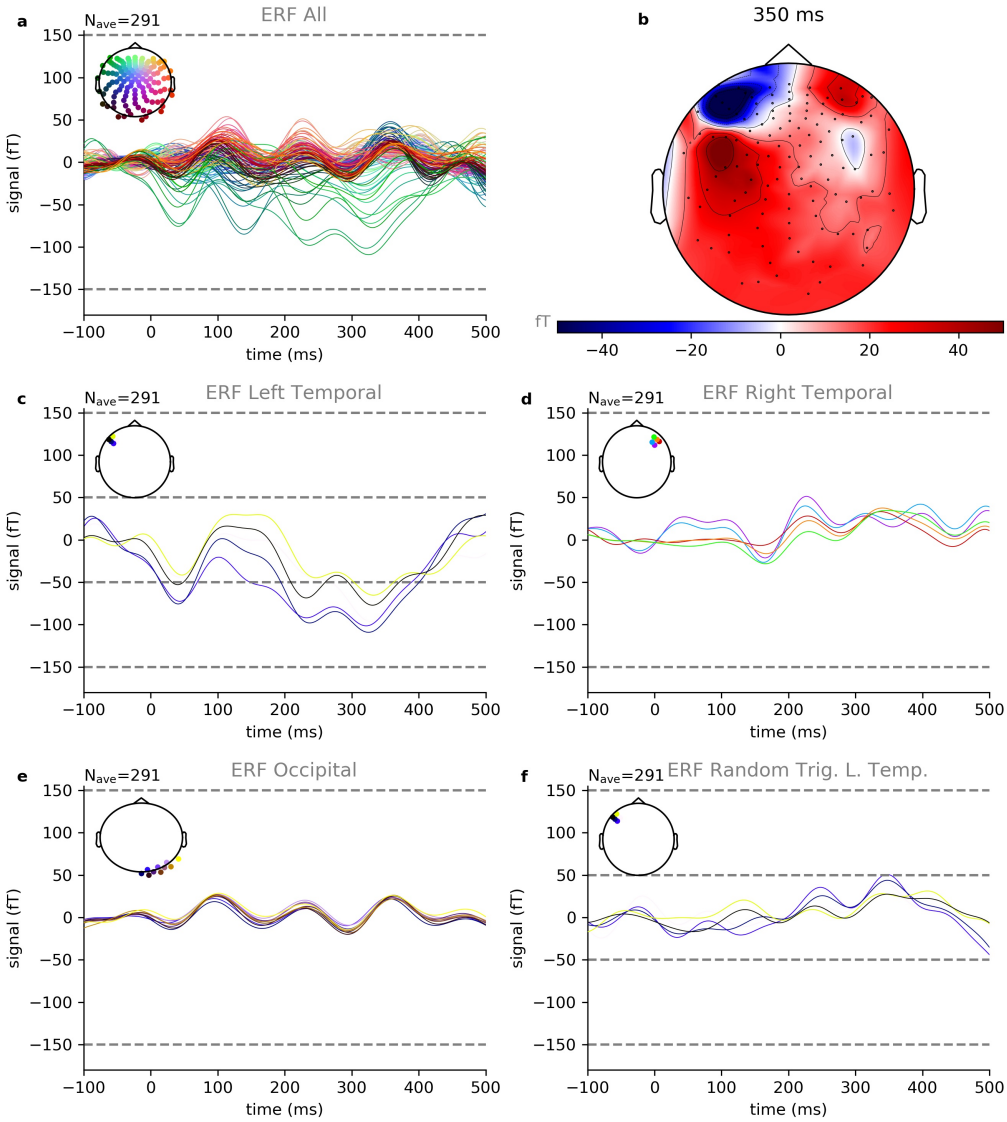

Figure 6: **Event related fields for word onset.** Shown are exemplary data of book parts number 1-3 of 10 from subject 2 of 15. a: Summary of ERFs of all 248 recording channels averaged over 291 trials. Colors indicate the positions of the recording channels. b: Spatial distribution of ERF amplitudes at 350ms after word onset. c: The largest amplitudes occur in channels located at temporal and frontal areas of the left hemisphere. d: The corresponding channels at the right hemisphere show clearly smaller ERF amplitudes. e: The same is true for occipital channels. f: Same channels as in c, but averaged over randomly chosen triggers instead of word onset triggers. Also in this control condition, the resulting amplitudes are smaller than those for the word onset condition.

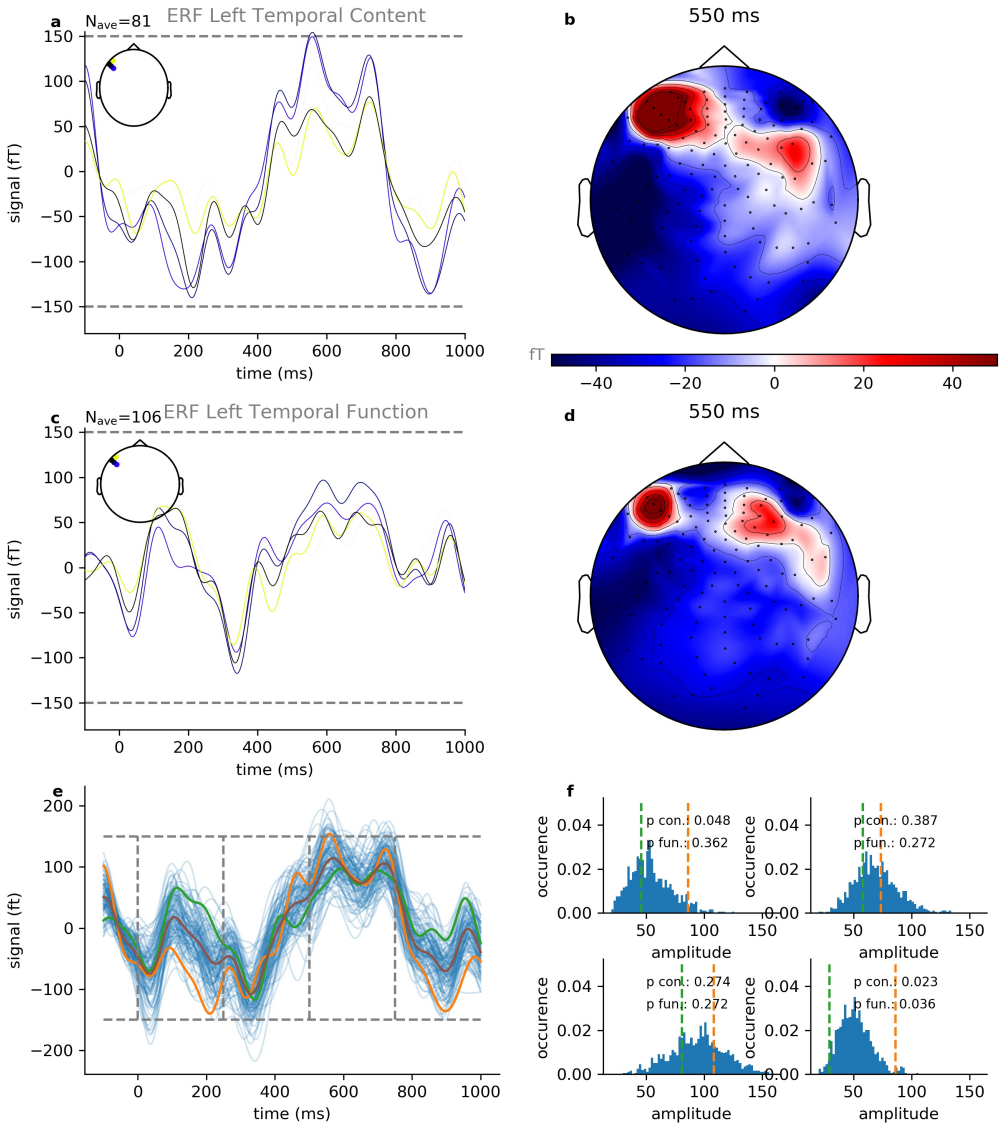

Figure 7: **Event related fields for function and content words.** Shown are exemplary data of book parts number 1-3 of 10 from subject 2 of 15. a: Averaged ERFs for content words (n=81 trials) with largest amplitudes. b: Spatial distribution of ERF amplitudes at 550ms after word onset for content words. c: Averaged ERFs for function words (n=106 trials) with largest amplitudes. d: Spatial distribution of ERF amplitudes at 550ms after word onset for function words. e: ERF with the largest amplitude for content words (orange) and function words (green), together with ERFs derived from permutation test (blue). f: Distribution of ERF amplitudes derived from permutation test within four subsequent time frames: $0\,ms$–$250\,ms$ (upper left), $250\,ms$–$500\,ms$ (upper right), $500\,ms$–$750\,ms$ (lower left) and $750\,ms$–$1000\,ms$ (lower right).

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Additional Information

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Competing interests

The authors declare no competing financial interests.

Author contributions

PK and AS designed the study. AS, PK and VK prepared the stimulation and processed the audiobook. VK, MH, AS and PK performed the experiments. AS and PK analyzed the data. AS, PK and KS analyzed the text of the novel. AS, PK, RT, MRHS, AM and PU discussed the results. PK, AS, RT, MRHS and PU wrote the manuscript.

Supplements

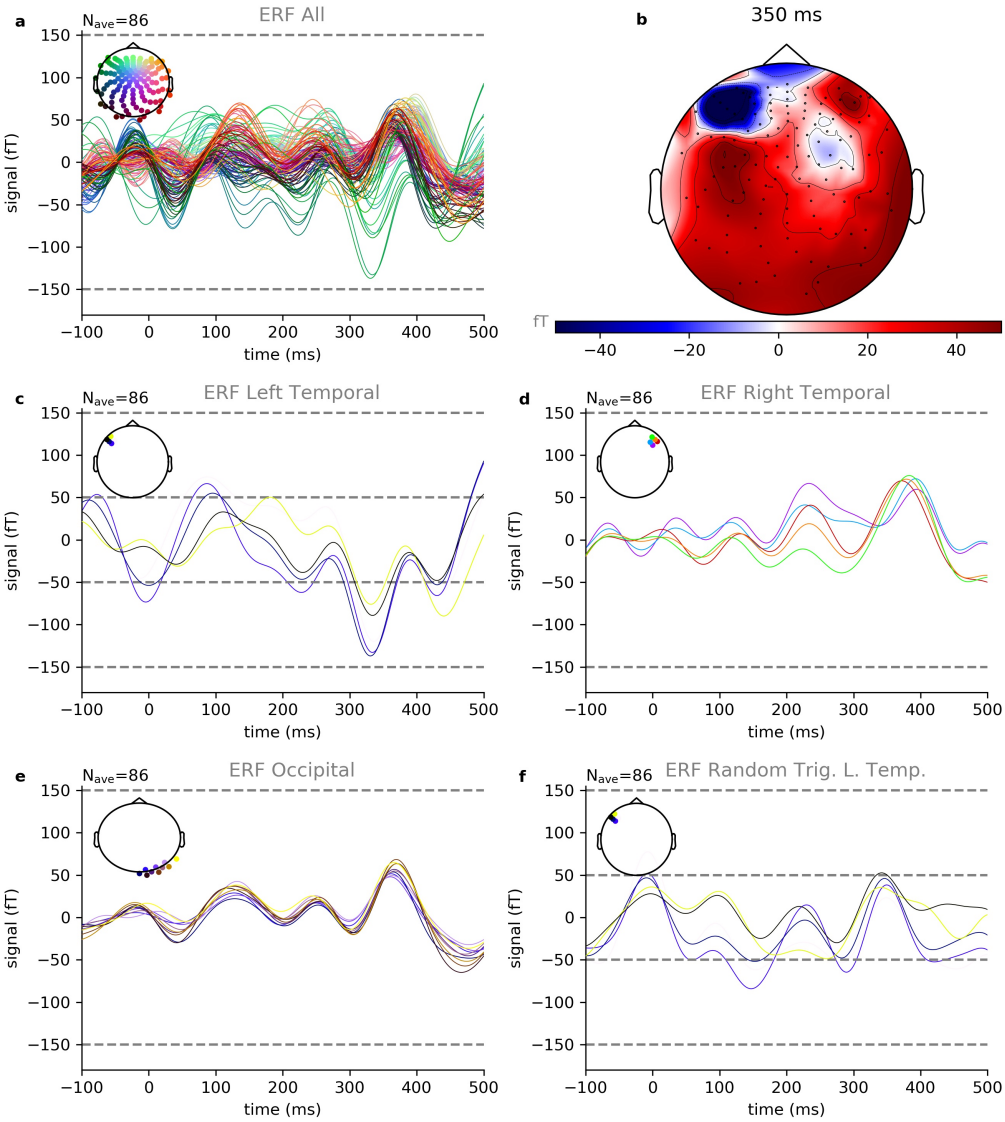

Figure S1: **Event related fields of word onsets. Sub-sample 1 of 3.** Shown are exemplary data of book part number 1 of 10 from subject 2 of 15. a: Summary of ERFs of all 248 recording channels averaged over 86 trials. Colors indicate the positions of the recording channels. b: Spatial distribution of ERF amplitudes at 350ms after word onset. c: The largest amplitudes occur in channels located at temporal and frontal areas of the left hemisphere. d: The corresponding channels at the right hemisphere show clearly smaller ERF amplitudes. e: The same is true for occipital channels. f: Same channels as in c, but averaged over randomly chosen triggers instead of word onset triggers. Also in this control condition, the resulting amplitudes are smaller than those for the word onset condition.

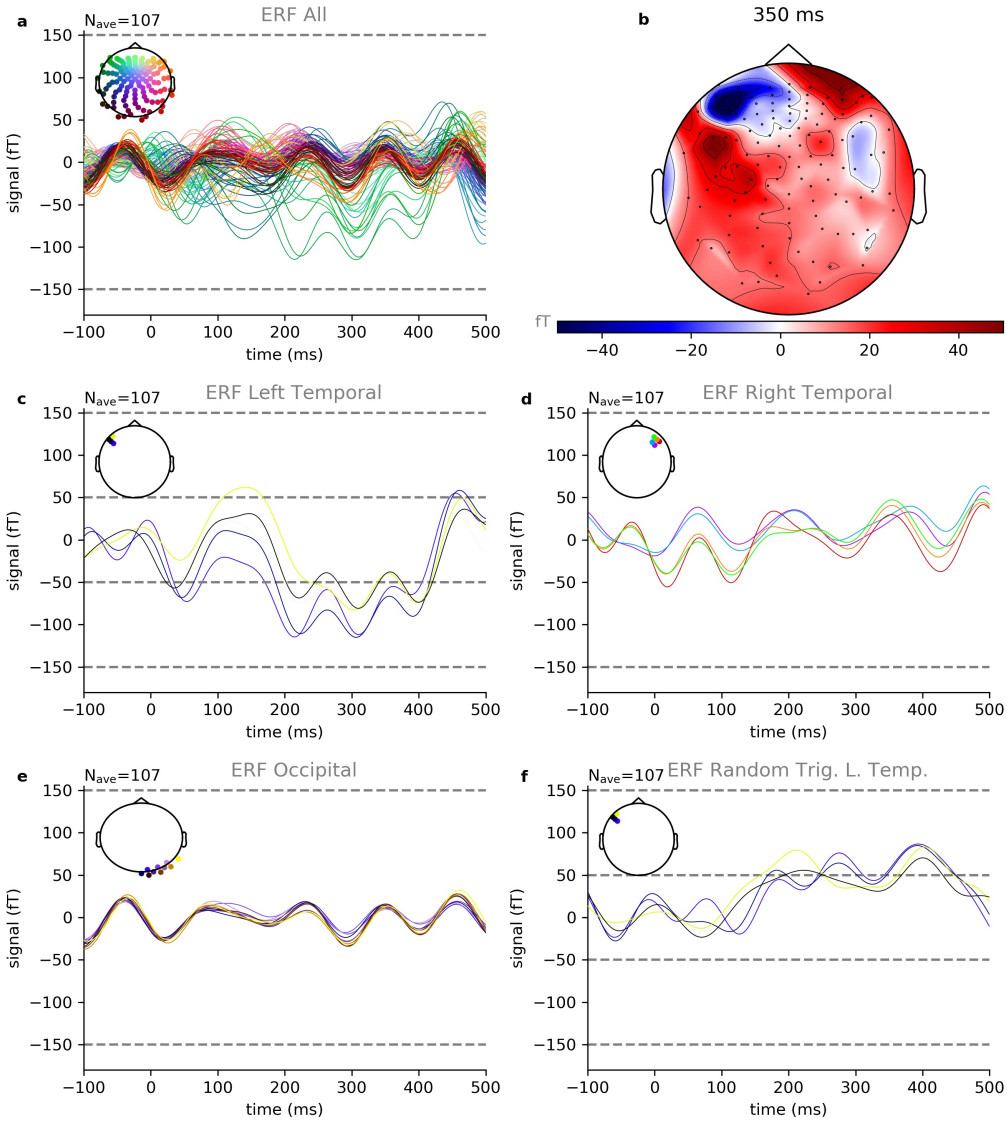

Figure S2: **Event related fields of word onsets. Sub-sample 2 of 3.** Shown are exemplary data of book part number 2 of 10 from subject 2 of 15. a: Summary of ERFs of all 248 recording channels averaged over 107 trials. Colors indicate the positions of the recording channels. b: Spatial distribution of ERF amplitudes at 350ms after word onset. c: The largest amplitudes occur in channels located at temporal and frontal areas of the left hemisphere. d: The corresponding channels at the right hemisphere show clearly smaller ERF amplitudes. e: The same is true for occipital channels. f: Same channels as in c, but averaged over randomly chosen triggers instead of word onset triggers. Also in this control condition, the resulting amplitudes are smaller than those for the word onset condition.

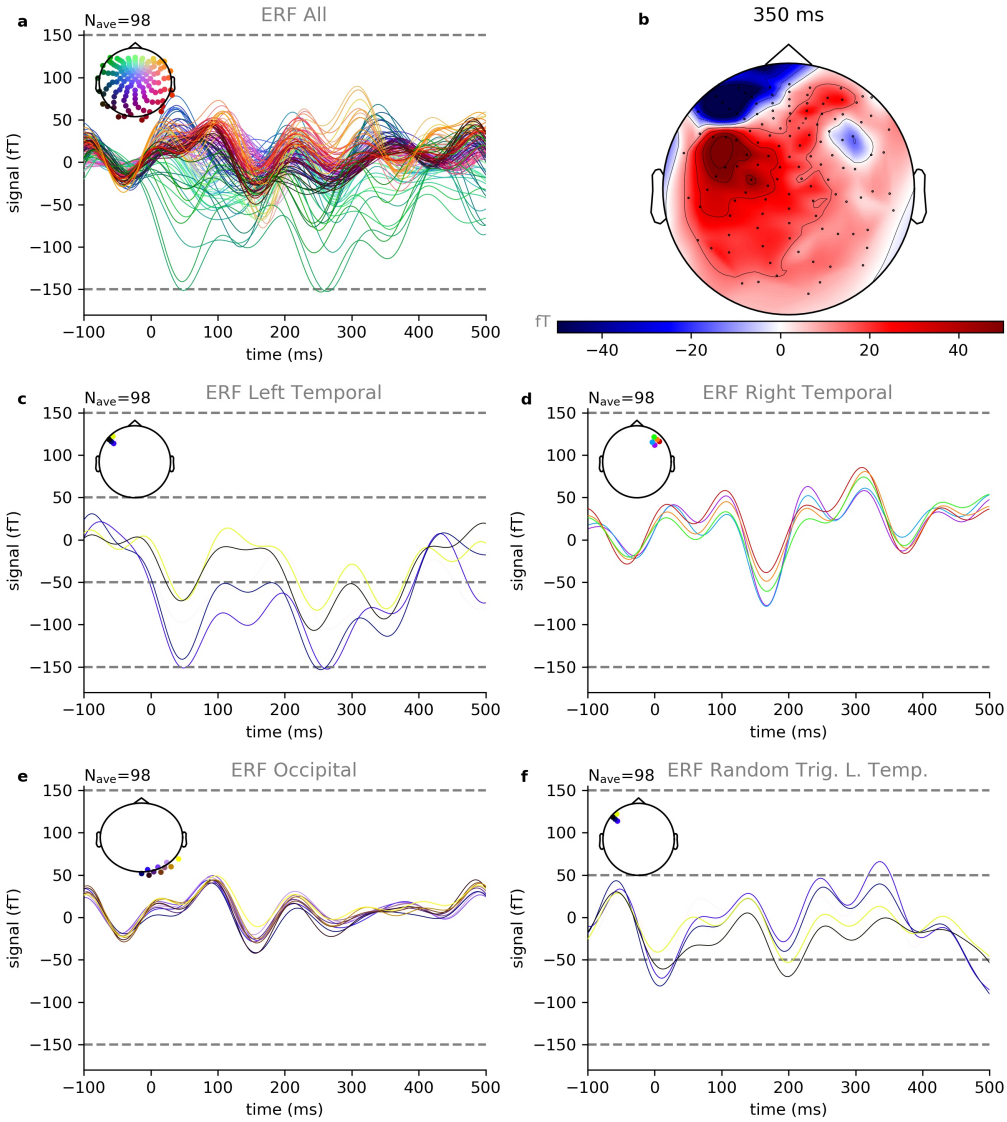

Figure S3: **Event related fields of word onsets. Sub-sample 3 of 3.** Shown are exemplary data of book part number 3 of 10 from subject 2 of 15. a: Summary of ERFs of all 248 recording channels averaged over 98 trials. Colors indicate the positions of the recording channels. b: Spatial distribution of ERF amplitudes at 350ms after word onset. c: The largest amplitudes occur in channels located at temporal and frontal areas of the left hemisphere. d: The corresponding channels at the right hemisphere show clearly smaller ERF amplitudes. e: The same is true for occipital channels. f: Same channels as in c, but averaged over randomly chosen triggers instead of word onset triggers. Also in this control condition, the resulting amplitudes are smaller than those for the word onset condition.

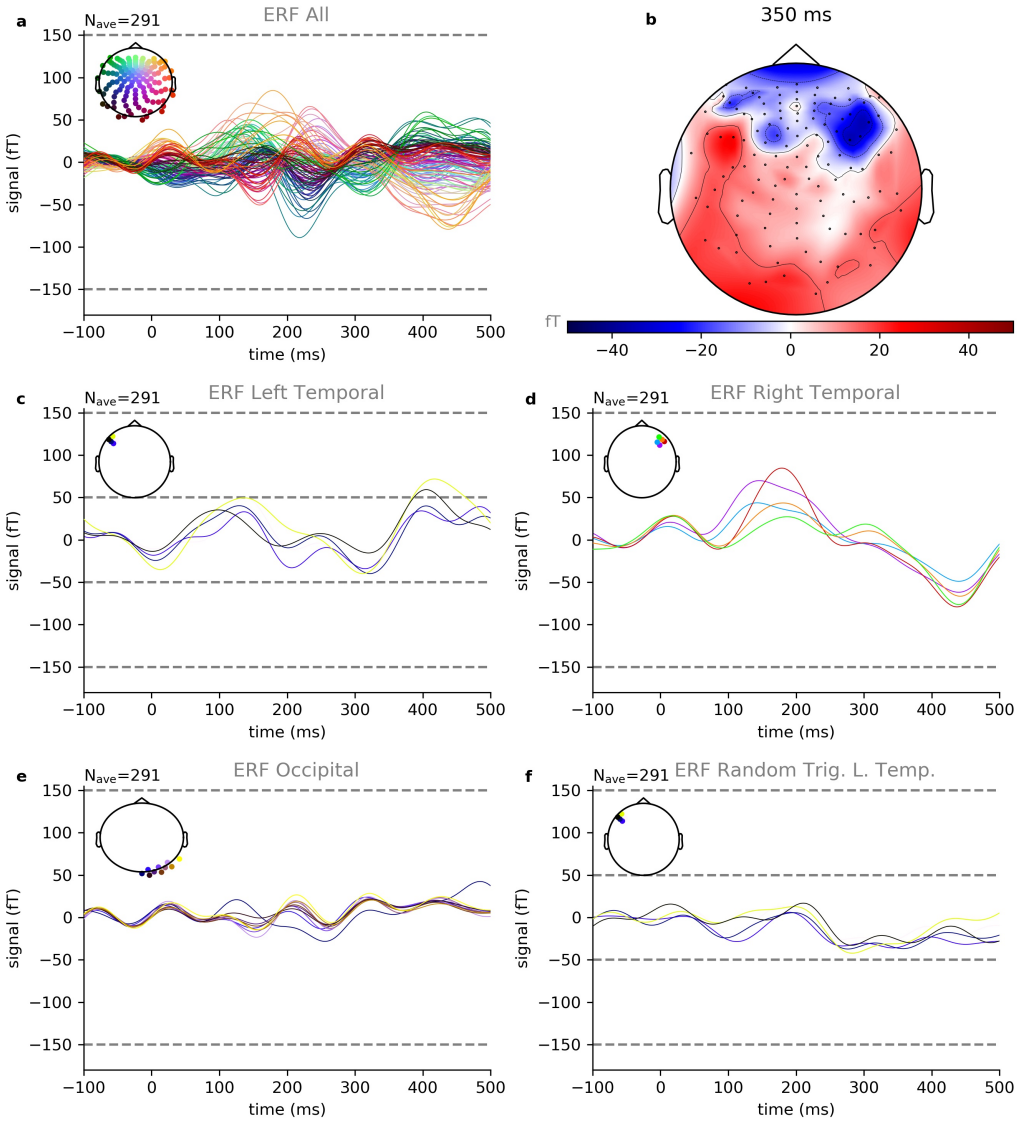

Figure S4: **Event related fields for word onset.** Shown are exemplary data of book parts number 1-3 of 10 from subject 5 of 15. a: Summary of ERFs of all 248 recording channels averaged over 291 trials. Colors indicate the positions of the recording channels. b: Spatial distribution of ERF amplitudes at 350ms after word onset. c: The largest amplitudes occur in channels located at temporal and frontal areas of the left hemisphere. d: The corresponding channels at the right hemisphere show clearly smaller ERF amplitudes. e: The same is true for occipital channels. f: Same channels as in c, but averaged over randomly chosen triggers instead of word onset triggers. Also in this control condition, the resulting amplitudes are smaller than those for the word onset condition.

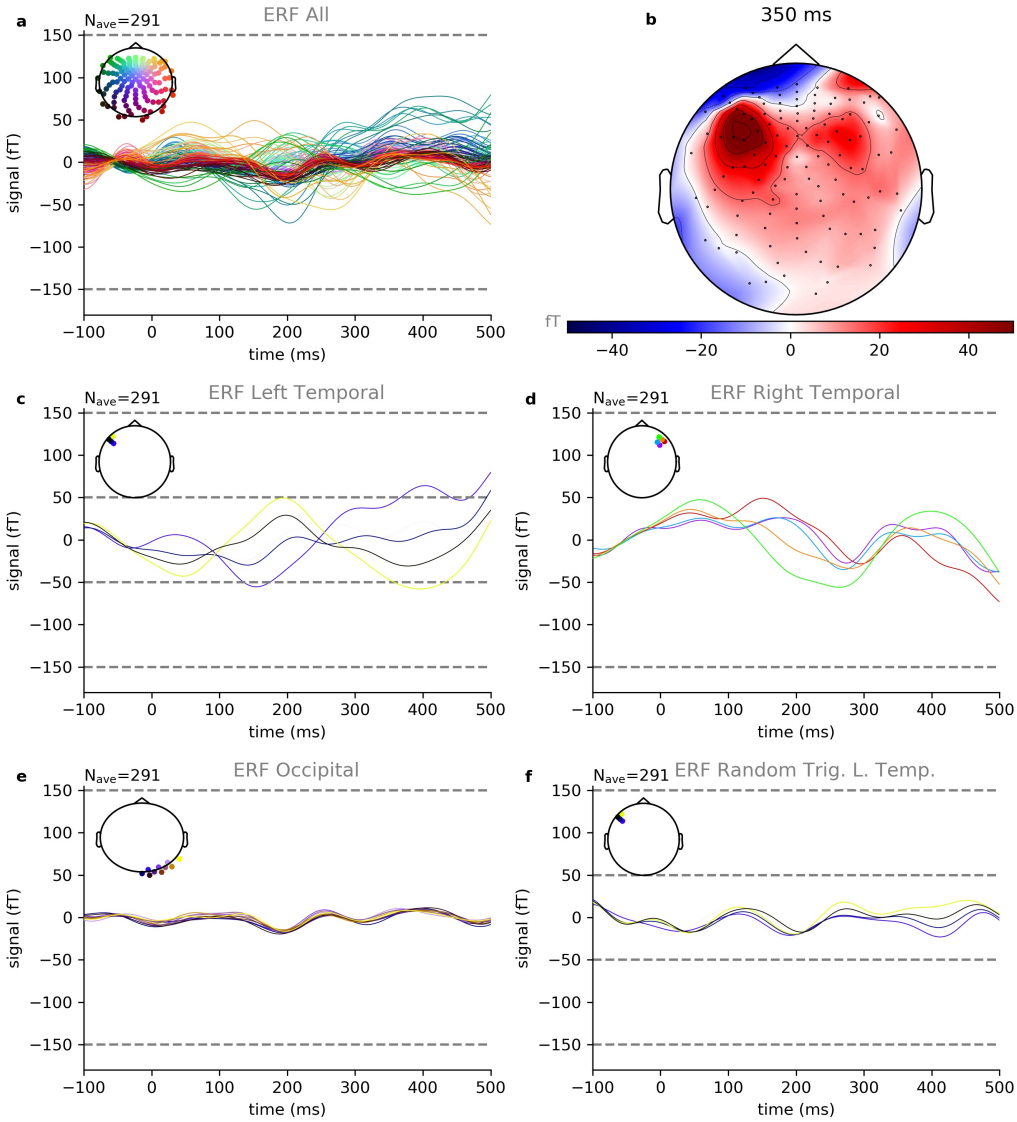

Figure S5: **Event related fields for word onset.** Shown are exemplary data of book parts number 1-3 of 10 from subject 8 of 15. a: Summary of ERFs of all 248 recording channels averaged over 291 trials. Colors indicate the positions of the recording channels. b: Spatial distribution of ERF amplitudes at 350ms after word onset. c: The largest amplitudes occur in channels located at temporal and frontal areas of the left hemisphere. d: The corresponding channels at the right hemisphere show clearly smaller ERF amplitudes. e: The same is true for occipital channels. f: Same channels as in c, but averaged over randomly chosen triggers instead of word onset triggers. Also in this control condition, the resulting amplitudes are smaller than those for the word onset condition.

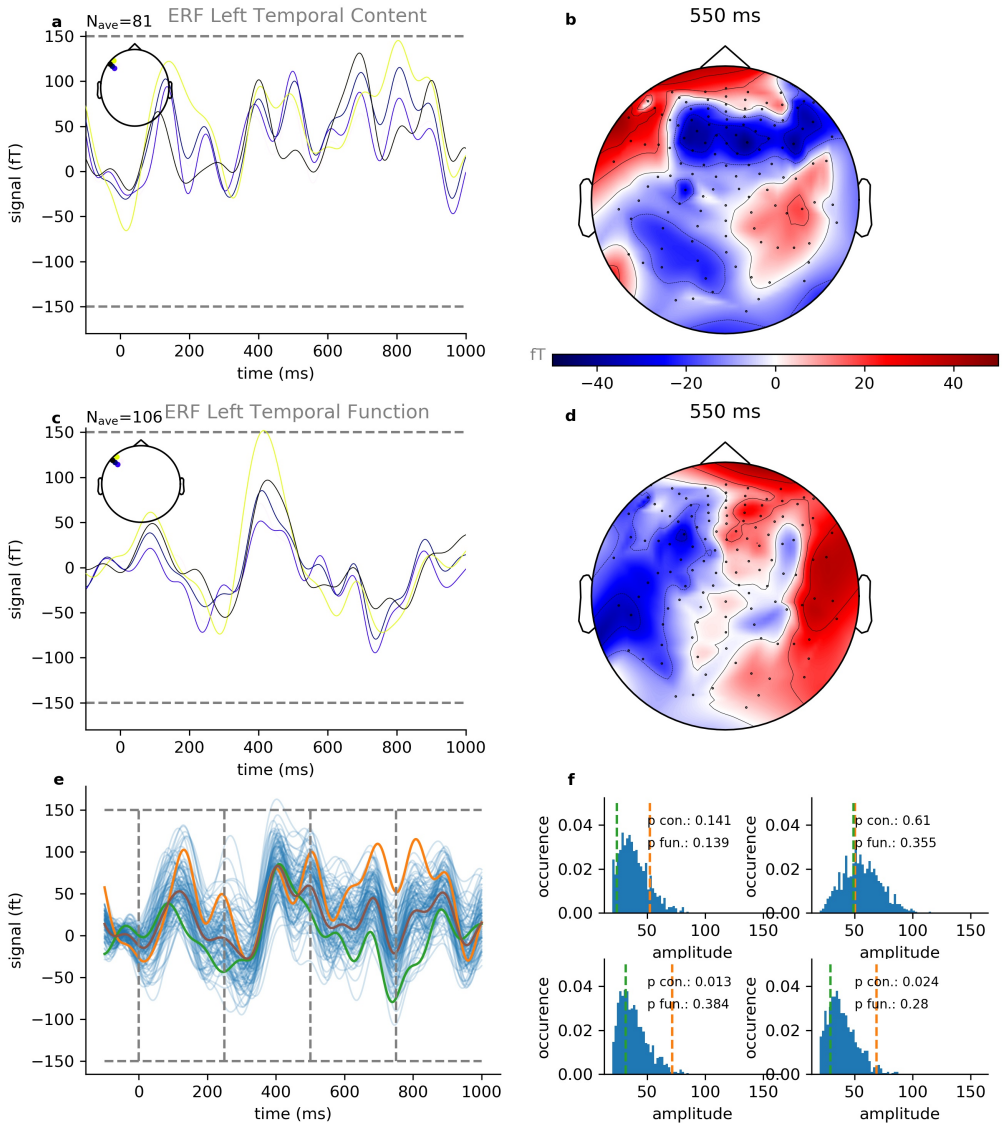

Figure S6: **Event related fields for function and content words.** Shown are exemplary data of book parts number 1-3 of 10 from subject 5 of 15. a: Averaged ERFs for content words (n=81 trials) with largest amplitudes. b: Spatial distribution of ERF amplitudes at 550ms after word onset for content words. c: Averaged ERFs for function words (n=106 trials) with largest amplitudes. d: Spatial distribution of ERF amplitudes at 550ms after word onset for function words. e: ERF with the largest amplitude for content words (orange) and function words (green), together with ERFs derived from permutation test (blue). f: Distribution of ERF amplitudes derived from permutation test within four subsequent time frames: $0\,ms$–$250\,ms$ (upper left), $250\,ms$–$500\,ms$ (upper right), $500\,ms$–$750\,ms$ (lower left) and $750\,ms$–$1000\,ms$ (lower right).

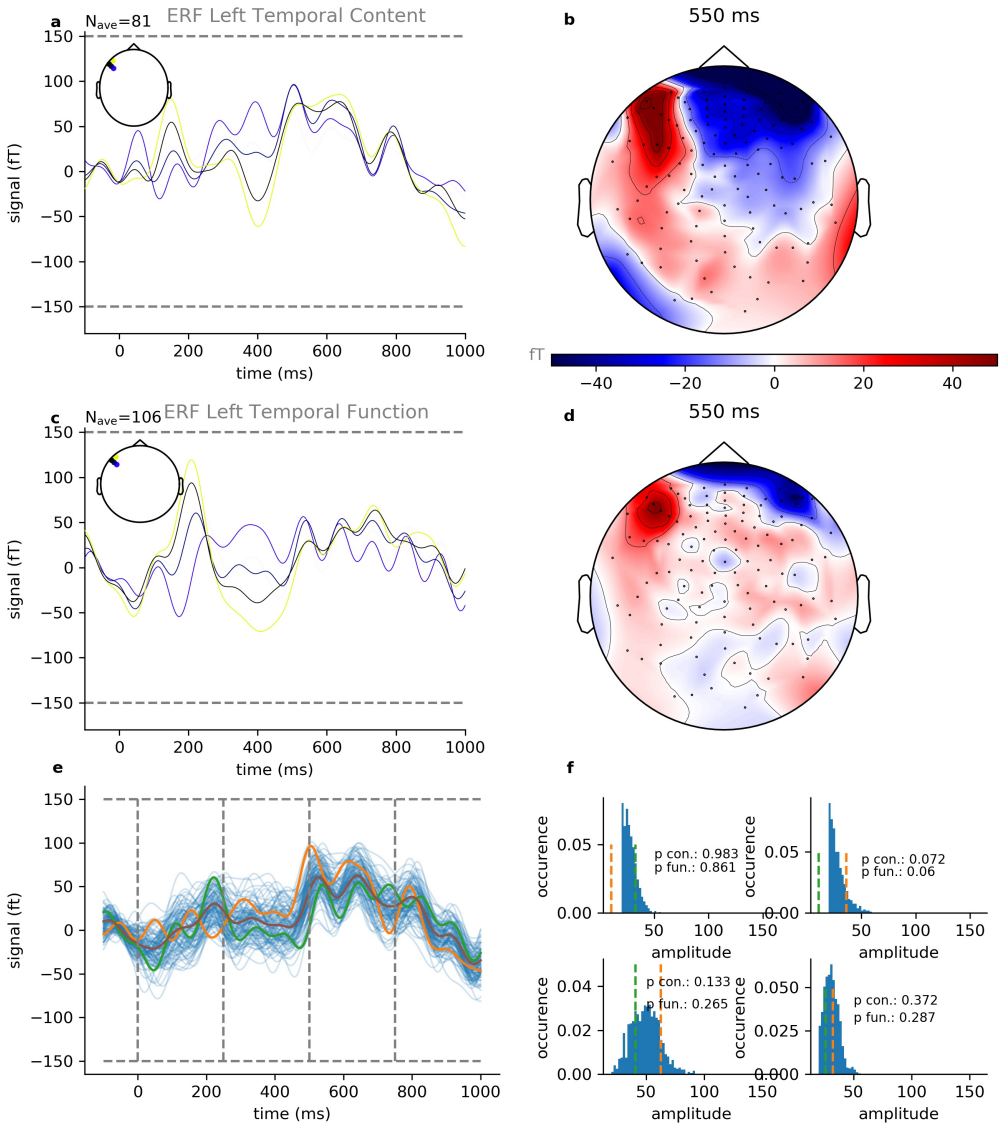

Figure S7: **Event related fields for function and content words.** Shown are exemplary data of book parts number 1-3 of 10 from subject 8 of 15. a: Averaged ERFs for content words (n=81 trials) with largest amplitudes. b: Spatial distribution of ERF amplitudes at 550ms after word onset for content words. c: Averaged ERFs for function words (n=106 trials) with largest amplitudes. d: Spatial distribution of ERF amplitudes at 550ms after word onset for function words. e: ERF with the largest amplitude for content words (orange) and function words (green), together with ERFs derived from permutation test (blue). f: Distribution of ERF amplitudes derived from permutation test within four subsequent time frames: $0\,ms$–$250\,ms$ (upper left), $250\,ms$–$500\,ms$ (upper right), $500\,ms$–$750\,ms$ (lower left) and $750\,ms$–$1000\,ms$ (lower right).

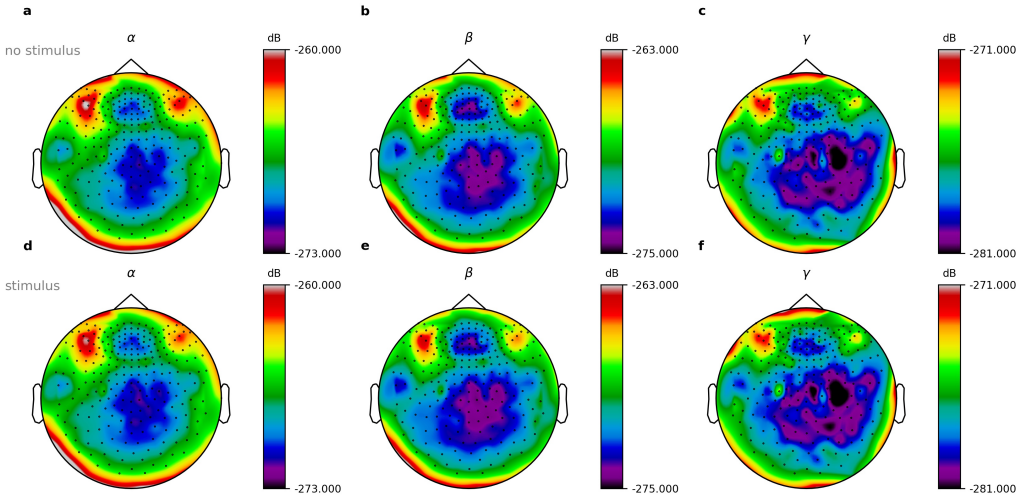

Figure S8: **Normalized power spectra for words and silence.** Shown are exemplary data of book parts number 1-3 of 10 from subject 2 of 15. a-c: Power spectra for word offset, i.e. silence. d-f: Power spectra for word onsets. a,d: Alpha frequency range. b,e: Beta frequency range. c,f: Gamma frequency range.

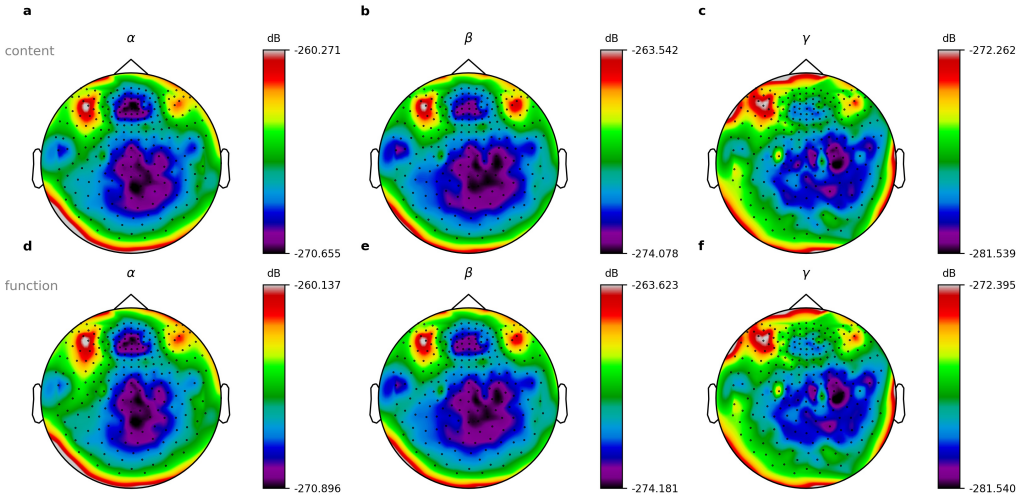

Figure S9: **Normalized power spectra for content and function words.** Shown are exemplary data of book parts number 1-3 of 10 from subject 2 of 15. a-c: Power spectra for content words. d-f: Power spectra for function words. a,d: Alpha frequency range. b,e: Beta frequency range. c,f: Gamma frequency range.

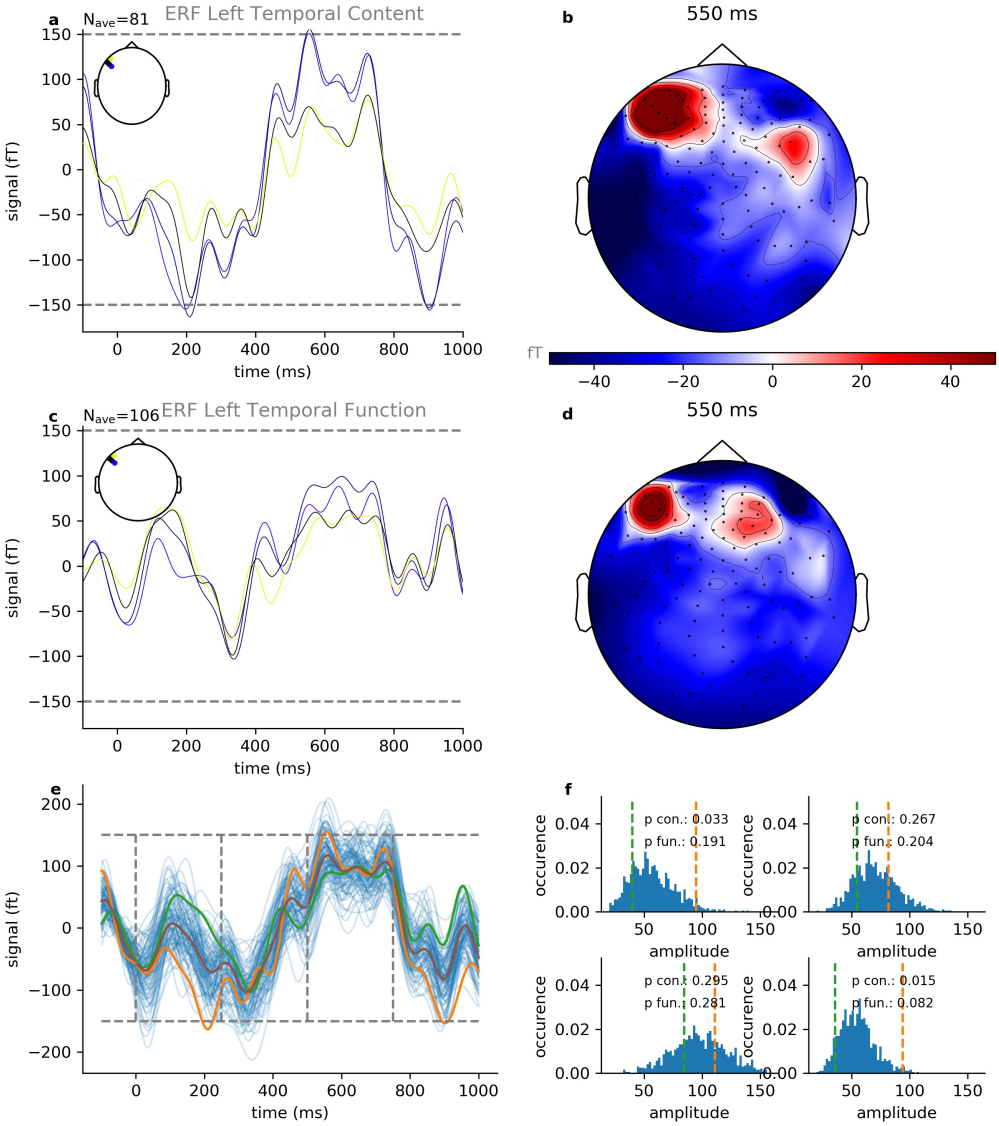

Figure S10: **Event related fields for function and content words.** Shown are the same analyses and participant as in Figure 7. However, for these analyses we did not delete the first two independent components. As the results are qualitatively equal, this does not affect the difference of neural responses to content and function words.